

Eye size in birds and the timing of song at dawn

Robert J. Thomas¹, Tamás Székely^{2*}, Innes C. Cuthill¹,
David G. C. Harper³, Stuart E. Newson⁴, Tim D. Frayling⁵
and Paul D. Wallis⁶

¹Centre for Behavioural Biology, School of Biological Sciences, University of Bristol, Bristol BS8 1UG, UK

²Department of Biology and Biochemistry, University of Bath, Claverton Down, Bath BA2 7AY, UK

³School of Biological Sciences, University of Sussex, Falmer, East Sussex BN1 9QG, UK

⁴British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK

⁵British Trust for Conservation Volunteers, Cayley Hall, Shepherd Road, Gloucester GL2 5DW, UK

⁶24 Jireh Court, Perry Mount Road, Haywards Heath, West Sussex RH16 3BH, UK

Why do different species of birds start their dawn choruses at different times? We test the hypothesis that the times at which different species start singing at dawn are related to their visual capability at low light intensities. Birds with large eyes can achieve greater pupil diameters and hence, all other things being equal, greater visual sensitivity and resolution than birds with small eyes. We estimated the maximum pupil diameter of passerine birds by measuring the diameter of the exposed eye surface, and measured the times of the first songs at dawn of songbirds present in different bird communities, and the light intensities at these times. Using phylogenetic comparative analyses, we found that songbirds with large eyes started to sing at lower light intensities (and therefore earlier) than species with smaller eyes. These relationships were stronger when differences in body size were controlled for statistically, and were consistent between two phylogenies and when species were treated as independent data points. Our results therefore provide robust support for the hypothesis that visual capability at low light levels influences the times at which birds start to sing at dawn.

Keywords: dawn chorus; eye size; song; light intensity; songbirds

1. INTRODUCTION

One of the most striking features of the dawn chorus in any bird community is that different species start to sing at different times. For example, in a Welsh woodland in spring, common redstarts *Phoenicurus phoenicurus* begin to sing well before the first light of dawn is detectable to the human observer (this study). As dawn breaks, European robins *Erithacus rubecula*, common blackbirds *Turdus merula*, song thrushes *Turdus philomelos* and pied flycatchers *Ficedula hypoleuca* join the chorus in turn, followed by a succession of other species. By the time birds such as chaffinches *Fringilla coelebs* and blue tits *Parus caeruleus* begin to sing, the earliest species are already beginning to fall silent. Species may differ by as much as 100 min in the timing of their first song (see § 3). Whilst there are many theories for why the dawn chorus exists (reviewed by Mace 1987; Staicer *et al.* 1996), few have attempted to explain the interspecific differences that are so characteristic of its onset. We test one possible explanation: differences in visual capability in low light.

This sequential order of the start of the dawn chorus has been well known for a long time (e.g. Allard 1930; Leopold & Eynon 1961), but the reason for the staggered start has remained unexplained. Armstrong (1963) noted that some species such as European robins, which start their dawn choruses early, have bigger eyes than species such as house sparrows *Passer domesticus*, which start their dawn choruses late. He suggested that the order in which

species start to sing is related to differences between species in the ability to see at low light intensities: birds should delay singing at dawn until they can see well enough to carry out important behaviours related to song, such as territorial aggression and courtship. Singing may reveal the position of the bird (Krams 2001), and thus singing birds may need vision to detect predators. Kacelnik (1979) and Kacelnik & Krebs (1982) also implicated light intensity in the timing of the dawn chorus, but in the context that song is timed to avoid overlap with visually mediated foraging. Kacelnik (1979) provided experimental evidence that great tits *Parus major* only forage profitably at light intensities higher than those at which the dawn chorus ends in this species.

Martin (1993) reviewed the principles of eye design for vision at low light intensities. The minimum light intensity at which a bird's behaviour can be visually guided will depend on both its ability to detect light of low intensity (visual sensitivity) and its ability to distinguish detail at a given light intensity (visual resolution) (Snyder *et al.* 1977; Barlow 1981). Visual sensitivity can be increased by increasing the pupil aperture and/or by increasing the length of the visual receptors. An increase in pupil aperture will only increase visual sensitivity without a loss of visual resolution up to a certain limit (0.5 of the focal length of the eye). Above this limit, visual sensitivity can be further increased without a loss of visual resolution by coupling an increase in aperture with an increase in focal length and receptor diameter (Miller 1979; Land 1981).

Visual resolution can be increased by decreasing the diameter of the visual receptors and/or by increasing focal length. In order to increase resolution without a loss of

* Author for correspondence (t.szekely@bath.ac.uk).

visual sensitivity, the increase in focal length must be coupled with an increase in pupil aperture (Land 1981). Therefore, the evolution of eyes in the direction of greater sensitivity without a loss of visual resolution, or of greater resolution without a loss of visual sensitivity, requires an increase in pupil aperture and hence an increase in eye size (Land 1981). In other words, whether visual sensitivity or visual resolution is most limiting to activity when light intensity is low, the size of an animal's eyes will affect its visual capabilities at low light intensities (Hughes 1977; Martin 1993; Motani *et al.* 1999).

As well as the benefits of better vision, there are, however, costs associated with having large eyes, such as the increased flight costs a flying animal incurs by carrying a larger payload (Laughlin 1995), the energetic cost of manufacturing and maintaining the many millions of nerve cells (Laughlin *et al.* 1998), and possibly an increased risk of damage to the eye (Harper 1988). The size of an animal's eyes is likely to be a reflection of these costs and benefits (Motani *et al.* 1999). Birds are highly visually guided animals, so we predicted that the timing of activity is related to eye size in birds. Indeed, other studies have described relationships between visual capabilities (including eye size), foraging strategy, and the timing of foraging in shorebirds (Rojas *et al.* 1999; R. J. Thomas *et al.*, unpublished data).

In the present study, we tested the hypothesis that the times at which different species start singing at dawn are influenced by their visual capacity at low light intensities (Armstrong 1963; Kacelnik 1979). To do this, we investigated the relationships between eye size, and the times and light intensities at which different species start to sing in several bird communities. When low light constrains vision, a bird should open its pupil to the maximum aperture possible. The pupil aperture obviously cannot usefully be wider than the transparent area of the exposed eye surface through which photons can pass. We therefore used the diameter of a bird's exposed eye surface as a non-invasive estimate of its maximum pupil diameter and hence of its ability to detect and resolve images at low light intensities. The diameter of the exposed eye surface appears to be a better estimate of maximum pupil aperture than the volume of the eyeball, as used in studies based on measurements from skulls (e.g. Brooke *et al.* 1999; R. J. Thomas *et al.*, unpublished data). An advantage of our measurement is that it can be taken from live birds, for instance if the birds are captured for ringing. Measurements of eye size made using these two methods are compared below (see § 2). In order to avoid any effects of differences between avian orders in the characteristics of the eye other than eye size, we used only species from a single order: the passerine birds.

2. METHODS

(a) *Morphometric measurements*

R.J.T. measured the eye size and body mass of 57 species of wild passerine birds caught for ringing between October 1995 and June 1997 at various sites in the UK and Portugal (see electronic Appendix A, available on The Royal Society's Publications Web site). Dial callipers were used to measure (to 0.1 mm) the maximum diameter of the exposed eye surface, between the eyelids and mucous membrane surrounding the

eye. Care was taken not to touch the eye surface with the callipers. Body mass was measured to 0.1 g using a Salter spring balance, or a Salter electronic balance. The eye size measurements were very highly repeatable within species (Harper 1994), based on a total of 530 measurements from 43 species for which more than two individuals were measured (intraclass correlation coefficient, $r_1 = 0.970$, $F_{42,487} = 389.857$, $p < 0.001$).

\log_{10} (eye size) was highly correlated with \log_{10} (body mass) ($r = 0.892$, $n = 57$ species, $p < 0.001$). To test for effects of eye size independently from the effects of body size, we also included body size in multivariate models. Other studies have also described allometric relationships between eye size (based on measurements of the volume of eye sockets) and body size (Brooke *et al.* 1999). For comparison, in our dataset the coefficient from the regression of \log (eye size³) on \log (body mass) was 0.788 based on ordinary least-squares regression (OLS) and 0.883 based on reduced major-axis regression (RMA). Brooke *et al.* (1999) do not provide data for variation among the passerines, but the coefficients based on our dataset fall within the range of coefficients cited by Brooke *et al.* for five avian orders (OLS: 0.656–0.848; RMA: 0.720–0.946). The similarity of these coefficients, based on different methods of measuring eye size, reassures us that the measurement of the exposed eye surface used in our study provides a reliable estimate of overall eye size.

(b) *Measuring the start of the dawn chorus*

We recorded the times at which each species started to sing at dawn at seven study sites.

- (i) Site 1: Chew Valley Lake, Somerset, England (51°20' N, 2°40' W); lakeside mixed woodland, scrub, *Phragmites* reedbed, and hay meadows. Twenty-three songbird species. Five visits on consecutive days from 11 May to 15 May 1999.
- (ii) Site 2: Gwaelod y Garth, South Glamorgan, Wales (51°20' N, 2°40' W); oak (*Quercus*) and coniferous woodlands, improved grassland, and upland heath. Eighteen songbird species. Five visits on consecutive days from 17 May to 21 May 1999.
- (iii) Site 3: Pwllgloyw, Powys, Wales (49°0' N, 3°26' W); deciduous woodland, unimproved and improved grassland. Eleven songbird species. Six visits between 17 May and 20 June 1996.
- (iv) Site 4: Stanmer Park, Sussex, England (49°53' N, 0°4' W); deciduous woodland, hay meadows and arable fields. Twelve songbird species. Six visits between 5 April and 16 May 1995.
- (v) Site 5: Ashcombe Bottom, Sussex, England (49°54' N, 0°4' W); downland scrub and deciduous woodland adjoining chalk grassland. Twelve songbird species. Six visits between 13 May and 6 June 1996.
- (vi) Site 6: Quinta da Rocha, Algarve, Portugal (37°8' N, 8°44' W); gardens, *Citrus* orchards, scrub and arable fields. Fifteen songbird species. Six visits between 4 March and 28 March 1996.
- (vii) Site 7: Guarda, Graubünden, Switzerland (46°48' N, 9°21' E); deciduous and coniferous woodland, and alpine hay meadows. Eight songbird species. Six visits between 30 June and 6 July 1996.

We arrived at each study site at least 2 h before sunrise; i.e. before any diurnal species had started to sing. We then recorded

Table 1. Comparative analyses by phylogenetically independent contrasts of eye size, body mass, light intensity and timing of first song. Least-squares regression analyses with regressions forced through zero (see § 2).

| model | explanatory variable(s) | regression coefficient | <i>F</i> (d.f.) | <i>p</i> | η^2 |
|---|-------------------------|------------------------|-----------------|----------|----------|
| dependent variable: light intensity at time of first song | | | | | |
| site 1 | | | | | |
| model 1 | eye size ^a | -15.299 | 3.297 (1,21) | 0.084 | 0.136 |
| model 2 | eye size | -57.099 | 16.391 (1,20) | 0.001 | 0.450 |
| | body mass | 14.295 | 11.525 (1,20) | 0.003 | 0.366 |
| site 2 | | | | | |
| model 1 | eye size | -17.431 | 8.043 (1,16) | 0.012 | 0.335 |
| model 2 | eye size | -38.734 | 15.735 (1,15) | 0.001 | 0.512 |
| | body mass | 7.759 | 6.721 (1,15) | 0.020 | 0.309 |
| dependent variable: time of first song | | | | | |
| model 1 | eye size ^b | -62.719 | 1.316 (1,36) | 0.259 | 0.035 |
| model 2 | eye size | -225.584 | 5.709 (1,35) | 0.022 | 0.140 |
| | body mass | 53.009 | 4.295 (1,35) | 0.046 | 0.109 |
| dependent variable: adjusted time of first song | | | | | |
| model 1 | eye size ^c | -78.810 | 2.235 (1,36) | 0.144 | 0.058 |
| model 2 | eye size | -248.177 | 7.581 (1,35) | 0.009 | 0.178 |
| | body mass | 59.757 | 5.095 (1,35) | 0.030 | 0.127 |

^a Power is 0.410.^b Power is 0.210.^c Power is 0.307.

the times at which each species was first heard singing, until we had heard all songbirds expected to be present at the site.

At sites 1 and 2, we measured ambient light intensity (in lux) using a TES 1330 digital light meter by positioning it horizontally 2 m above ground level, at least 25 m from the nearest cover, and with the light detector facing vertically upwards. Although photometric measures (e.g. lux) are not strictly appropriate for birds due to differences in spectral sensitivity between birds and humans (Endler 1990; Bennett *et al.* 1994), we expect our measurements to be a good first approximation (see Marchetti 1993). In addition, the many-orders-of-magnitude change in total light flux over the twilight period (Martin 1990) far surpasses those changes in spectral composition that might lead to biases in the estimate of the light available for bird vision.

Light intensity increased approximately linearly over the 90 min spanning the dawn chorus at sites 1 and 2 (R. J. Thomas, personal observations). Time of day can therefore be used as an index of the relative light intensities at which different species started singing at dawn. For each site the mean times or mean light intensities across all five to six dates were used.

To examine the generality of any association between visual capability and the onset of dawn song across a range of habitats and locations, we compared the times at which 38 species started singing at dawn at sites 1–7. Different bird communities were present at each site, but these sites had species in common. To make the start times comparable between sites, we recorded the time of day as minutes relative to civil dawn twilight (the point at which the sun is six degrees below the horizon, which occurs approximately midway through the sequential start of the dawn chorus in most bird communities). For each species, we then calculated the mean time of its first song, across all the sites at which it occurred.

We also analysed the start times by correcting for differences between sites in the times of the first songs relative to civil twilight. The site that had the most species in common with each

of the other sites was site 1. Thus we adjusted the times of the first songs of the species at each site by the difference in mean time of the first song for all species that the site had in common with site 1. We then calculated the adjusted mean time of the first song for each species, across all the sites at which it occurred.

The light intensity at the time of the first song of each species was highly repeatable within species between sites 1 and 2, based on 14 species that occurred at both sites ($r_i = 0.822$, $F_{13,14} = 5.605$, $p < 0.001$). Also, the mean time of first song of each species was significantly repeatable within species between sites 1–7, based on 21 species that occurred at two or more sites ($r_i = 0.633$, $F_{20,64} = 7.922$, $p < 0.001$).

Both the times of the first songs and the light intensities at these times were highly repeatable within species between days for a given site. For instance, at site 1, based on its 23 species: $r_{i(\text{time})} = 0.894$, $F_{22,92} = 43.337$, $p < 0.001$; $r_{i(\text{light})} = 0.906$, $F_{22,92} = 49.325$, $p < 0.001$, whereas at site 2, based on its 18 species: $r_{i(\text{time})} = 0.860$, $F_{17,72} = 30.844$, $p < 0.001$; $r_{i(\text{light})} = 0.897$, $F_{17,72} = 44.349$, $p < 0.001$.

In table 1 and electronic Appendix B we quote values for partial η^2 ; i.e. the proportion of total variability in the dependent variable that is accounted for by each independent variable when other independent variables in the model are controlled for. This statistic therefore allows the relative explanatory power of each independent variable to be assessed. For non-significant relationships we also report the statistical power ($1 - \beta$).

(c) Comparative analyses

Eye size and other traits are unlikely to have independent evolutionary origins (Harvey & Pagel 1991; Martins 1996), and thus closely related species may share the same characteristics due to common descent (niche conservatism; Harvey & Pagel 1991). To control for phylogenetic relatedness we used the phylogenetically independent contrast method of Felsenstein (1985) as



Figure 1. The phylogenetic hypothesis for songbirds used in the comparative analyses (see § 2 for justification).

implemented by the CAIC, v. 2 computer program of Purvis & Rambaut (1995). This program computes independent evolutionary contrasts between characters for species in a given phylogeny.

Our phylogenetic hypothesis was based upon the work by Sibley & Ahlquist (1990): DNA–DNA hybridization phylogeny, and it was augmented by recent molecular studies. Sibley & Ahlquist (1990, figs 369, 379–384) provided the topology and branch lengths for all genera except *Serinus*, *Saxicola* and *Miliaria*. *Serinus* is probably more closely related to *Carduelis* than to other finches (Cramp & Perrins 1994a), *Saxicola* is more closely related to *Phoenicurus* than to thrushes (Cramp 1988; Monroe & Sibley 1993), and corn bunting (*Miliaria calandra*) is classified along with other buntings (Emberizidae; Cramp & Perrins 1994b; Monroe & Sibley 1993). For *Sylvia* warblers we used a recent consensus tree of Shirihaei *et al.* (2001) that was based upon mitochondrial DNA sequences, DNA–DNA hybridization and phenotypic characters. *Parus major* and *P. caeruleus* are more closely related to each other than each of them are to *P. ater* (Slikas *et al.* 1996). *Phylloscopus collybita* and *P. trochilus* are sister species and together they form a sister group to *P. bonelli* (Helbig *et al.* 1995). For finches, we used the composite phylogeny of Badyaev (1997) that infers closer phylogenetic relationship between *Carduelis carduelis* and *C. chloris* than between either of them and *C. cannabina*. Phylogeny of buntings was based upon the mitochondrial DNA sequence of Lee *et al.* (2001). The phylogenetic hypothesis of our main analysis is shown in figure 1.

We are aware that the phylogenetic relationships of several passerine taxa, in particular finches (*Carduelis*, *Serinus*) and buntings (*Emberiza*, *Miliaria*), are not satisfactorily resolved. Nonetheless, the results of our comparative analyses are robust to the adopted phylogenetic hypothesis, because using an alternative phylogeny with a different topology for finches and buntings (see Monroe & Sibley 1993; Lo Valvo *et al.* 1997) does not change any of our conclusions (results not shown).

\log_{10} (eye size) and \log_{10} (body mass) were analysed. The phylogeny does not provide within-genus branch lengths, so in these cases we used branch lengths of one. All branch lengths were log transformed as suggested by Garland *et al.* (1992). Using unit branch lengths does not change any of our conclusions (results not given). An important assumption of the method of Felsenstein (1985) is that the absolute value of the contrasts should be independent of their standard deviation (Garland *et al.* 1992). Our variables satisfied this assumption. All regressions between phylogenetically independent contrasts were forced through the origin (Harvey & Pagel 1991).

Recently the phylogenetic comparative methods have been criticized (Price 1997; Martins 2000; Harvey & Rambaut 2000). To be conservative, we repeated all analyses at the species level, although none of our main conclusions were changed (see electronic Appendices B and C).

3. RESULTS

(a) *Eye size and light intensity at dawn song*

Both eye size and body mass accounted for a significant amount of variation in the light intensities at which different species started to sing (table 1; figure 2). Simple linear regression (table 1; model 1 analyses) showed that evolutionary increases in eye size were significantly associated with starting to sing at lower light intensities at site 2. This association was in the same direction, but marginally non-significant at site 1 (model 1, $p = 0.084$, power is 0.410).

Multiple regression of the contrasts in eye size and body mass on contrasts in light intensity (table 1; model 2 analyses) showed that evolutionary increases in eye size were associated with starting to sing at lower light intensities, when body mass was controlled for statistically. These multiple regression models also showed that evolutionary increases in body mass were associated with start-

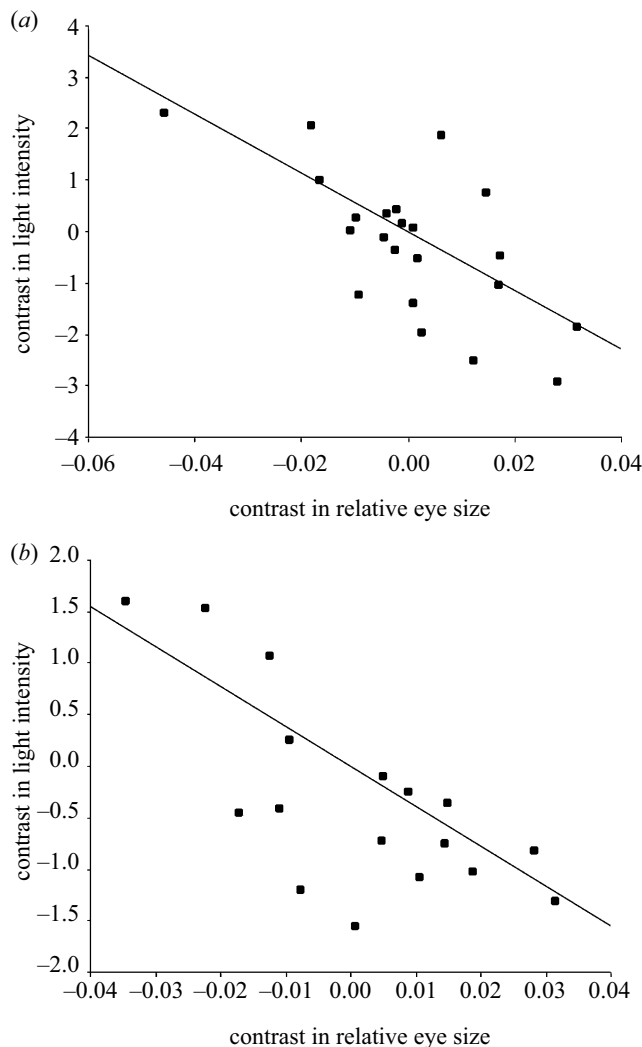


Figure 2. Relationships between phylogenetic contrasts in relative eye size and light intensity at first song at dawn in songbirds; (a) site 1 ($r = -0.676$) and (b) site 2 ($r = -0.711$). Relative eye size is the residual from the contrasts in least-squares regression of \log_{10} (eye size) on \log_{10} (body mass). We use residuals for illustrative purposes only, as the analyses are based on actual explanatory variables rather than residuals (see § 2).

ing to sing at higher (i.e. brighter) light intensities, when eye size was controlled for statistically.

(b) Eye size and timing of dawn song

When time of day was used as a proxy measurement for the light intensity at the time of the first song, the association with eye size was still clearly detectable, but only when variation in body mass was controlled for statistically (table 1; model 2 analyses; figure 3). This was true regardless of whether time relative to civil twilight, or the adjusted time, was used in the analysis. Evolutionary increases in eye size were associated with starting to sing earlier at dawn, when body mass was controlled for statistically. Evolutionary increases in body mass were associated with starting to sing later, when eye size was controlled for statistically.

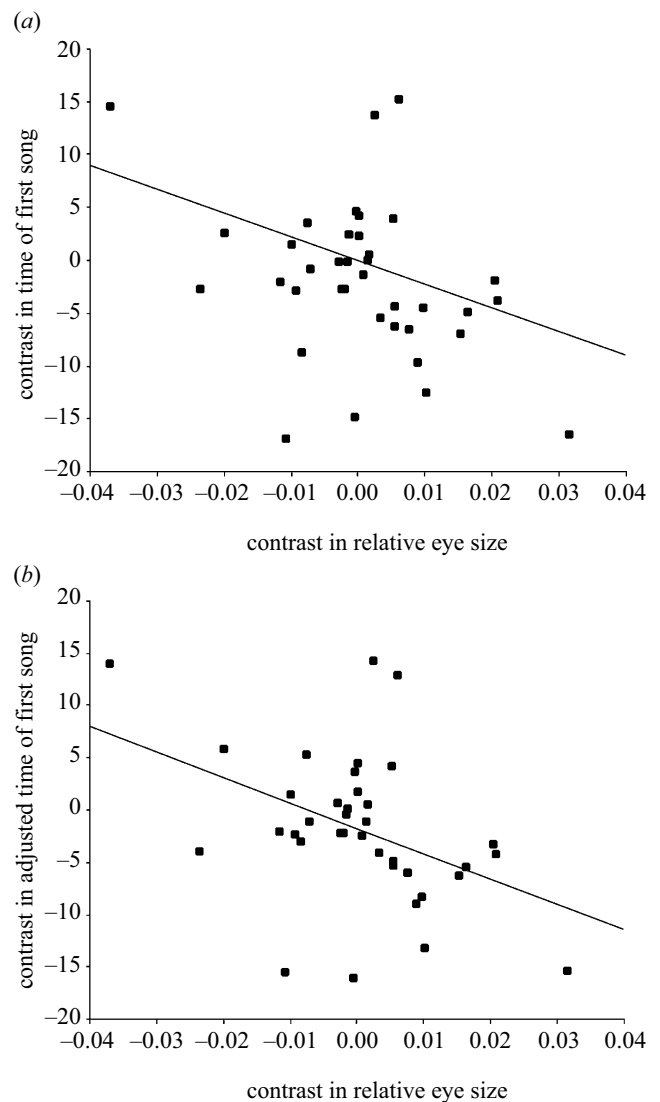


Figure 3. Relationships between phylogenetic contrasts in relative eye size and the timing of dawn song. (a) Time of first song ($r = -0.378$) and (b) adjusted time of first song ($r = -0.427$) (see § 2 and figure 2).

(c) Relative explanatory power of eye size and body mass

The partial η^2 values show that evolutionary changes in eye size accounts for a greater proportion of variation in starting light intensity (or the time of the first song) than did changes in body mass (table 1). Also, eye size accounts for a greater proportion of variation in starting light intensity (or the time of the first song) when body mass is taken into account (model 2 analyses), than when body mass is ignored (model 1 analyses). Thus variation in body mass tends to mask the relationship between eye size and the onset of song at dawn.

4. DISCUSSION

Our results show clearly that the light intensity at which the songbirds start singing at dawn is negatively associated with eye size (table 1; figures 2 and 3) and positively associated with body mass (table 1). Species that have larger eyes therefore start to sing at lower light intensities than species that have small eyes, as suggested by Armstrong

(1963). Eye size accounts for more variation in the start of the dawn chorus than body mass. These results are consistent whether species are treated as independent data points (electronic Appendix B), or if phylogeny is taken into account (table 1). These results are also consistent with the associations between eye size, body mass, and the time of the first song, found in a wide range of habitats and bird communities (table 1). Taken together, our results provide strong support for the hypothesis that the times at which different species join the dawn chorus is associated with their visual capability at low light intensities.

Visual capability may affect the timing of song directly, for example if birds start to sing only when they can see well enough to interact visually with conspecifics or avoid predators. Alternatively, the association may be indirect, for example if birds sing for a time at dawn until they are able to see well enough to begin foraging efficiently (Kacelnik 1979; Kacelnik & Krebs 1982).

Eye size and visual capability in birds are likely to be determined by a number of different selection pressures and constraints, and thus our results do not necessarily imply that large eyes have evolved to allow a bird to start singing earlier at dawn. For example, fast flight also requires good spatial resolution and hence large eyes (Leuckat's law: Hughes 1977; Brooke *et al.* 1999). The association of evolutionary changes in eye size with different behavioural and ecological traits (such as flight speed, foraging technique and vulnerability to predators) can be further investigated by future comparative analyses. For instance, directional comparative analyses are required to trace the history of changes between character states both in morphology and behaviour (Pagel 1997; Lindenfors & Tullberg 1998).

Body mass consistently explains a large proportion of the variation between species in the timing of dawn song when eye size is controlled for statistically: smaller birds begin to sing at lower light intensities than larger birds of equivalent eye size. There are two possible explanations for this unexpected association. First, a higher risk of overnight starvation may favour an earlier start to the day for smaller species. Diurnally active birds build up fat reserves over the course of the day, to fuel their metabolism overnight while they are unable to forage effectively (e.g. McNamara *et al.* 1994; Thomas 2000). Overnight metabolic costs can be considerable: for example, small birds commonly lose 5–10% of their total body mass overnight, and this can increase to 15% or more during long, cold winter nights (Thomas & Cuthill 2002). Metabolic rate scales allometrically, approximately as $(\text{body mass})^{0.72}$ in passerine birds (Alexander 1999), so smaller birds require larger energy reserves (relative to their body mass) than larger birds. As a result, the selective pressure favouring an earlier start to the active day may be stronger for smaller species. Our results, showing that body mass is positively associated with the time (or light intensity) at the start of dawn song, are consistent with this hypothesis.

Second, eye size relative to body mass, rather than absolute eye size may better explain visual capacity at low light intensities. If so, then either absolute eye size, or body mass, or both, may be significantly associated with the timing of song. Absolute pupil diameter is expected to influence visual acuity and resolution, as explained above

(see § 1). However, the precise factors determining the scaling of eye size to body mass are not fully understood (Brooke *et al.* 1999), and may have a bearing on the scaling of visual capability. For example, eye mass scales close to brain mass, suggesting that information-processing capacity could also constrain visual capability (Brooke *et al.* 1999).

The datasets obtained in the present study do not allow us to distinguish between these possibilities. However, future work should investigate these issues, for example by examining how eye size and body mass are associated with behavioural or physiological measures of visual capability (Rojas *et al.* 1999), or with the time of the onset of foraging at dawn (Kacelnik 1979).

R.J.T. was supported by a NERC studentship supervised by D.G.C.H., and by a NERC grant to I.C.C. and J. M. McNamara. Help with trapping birds was given in Portugal by the A Rocha Field Study Centre, and in the UK by the Llangorse Lake and Rye Bay Ringing Groups, Nicola Marples, John Hutchinson and Ed Drewitt. We are grateful to Mike Brooke, Colin Beale and Tim Roper for discussions, and to anonymous referees for comments on a previous draft of this manuscript.

REFERENCES

- Alexander, R. M. 1999 *Energy for animal life*. Oxford University Press.
- Allard, H. A. 1930 The first morning song of some birds of Washington, DC: its relation to light. *Am. Nat.* **64**, 436–469.
- Armstrong, E. A. 1963 *A study of bird song*. Oxford University Press.
- Badyaev, A. V. 1997 Altitudinal variation in sexual dimorphism: a new pattern and alternative hypotheses. *Behav. Ecol.* **8**, 675–690.
- Barlow, H. B. 1981 Critical limiting factors in the design of the eye and visual cortex. *Proc. R. Soc. Lond. B* **212**, 1–34.
- Bennett, A. T. D., Cuthill, I. C. & Norris, K. J. 1994 Sexual selection and the mismeasure of color. *Am. Nat.* **144**, 848–860.
- Brooke, M. D., Hanley, S. & Laughlin, S. B. 1999 The scaling of eye size with body mass in birds. *Proc. R. Soc. Lond. B* **266**, 405–412.
- Cramp, S. (ed) 1988 *The birds of the Western Palearctic*, vol. 5. Oxford University Press.
- Cramp, S. & Perrins, C. M. (eds) 1994a *The birds of the Western Palearctic*, vol. 8. Oxford University Press.
- Cramp, S. & Perrins, C. M. (eds) 1994b *The birds of the Western Palearctic*, vol. 9. Oxford University Press.
- Endler, J. A. 1990 On the measurement and classification of colour in studies of animal colour patterns. *Biol. J. Linn. Soc.* **41**, 315–352.
- Felsenstein, J. 1985 Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15.
- Garland Jr, T., Harvey, P. H. & Ives, A. R. 1992 Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* **41**, 18–32.
- Harper, D. G. C. 1988 Robin *Erithacus rubecula* species account. In *The birds of the Western Palearctic*, vol. 5 (ed. S. Cramp), p. 605. Oxford University Press.
- Harper, D. G. C. 1994 Some comments on the repeatability of measurements. *Ringing & Migration* **15**, 84–90.
- Harvey, P. H. & Pagel, M. D. 1991 *The comparative method in evolutionary biology*. Oxford University Press.
- Harvey, P. H. & Rambaut, A. 2000 Comparative analyses for adaptive radiations. *Phil. Trans. R. Soc. Lond. B* **355**, 1599–1605.
- Helbig, A., Seibold, I., Martens, J. & Wink, M. 1995 Genetic

- differentiation and phylogenetic relationships of Bonelli's warbler *Phylloscopus bonelli* and green warbler *P. nitidus*. *J. Avian Biol.* **26**, 139–153.
- Hughes, A. 1977 The topography of vision in mammals of contrasting life style: comparative optics and retinal organisation. In *Handbook of sensory physiology*, vol. VII/5 (ed. F. Crescitelli), pp. 613–756. Berlin: Springer.
- Kacelnik, A. 1979 The foraging efficiency of the great tit (*Parus major* L.) in relation to light intensity. *Anim. Behav.* **27**, 237–241.
- Kacelnik, A. & Krebs, J. R. 1982 The dawn chorus in the great tit (*Parus major*): proximate and ultimate causes. *Behaviour* **83**, 287–309.
- Krams, I. 2001 Communication in crested tits and the risk of predation. *Anim. Behav.* **61**, 1065–1068.
- Land, M. F. 1981 Optics and vision in invertebrates. In *Handbook of sensory physiology*, vol. VII/6B (ed. H. Autrum), pp. 471–592. Berlin: Springer.
- Laughlin, S. B. 1995 Towards the cost of seeing. In *Nervous systems and behaviour* (ed. M. Burrows, T. Matthews, P. L. Newland & H. J. Schuppe), p. 290. Stuttgart, Germany: Thieme.
- Laughlin, S. B., van Steveninck, R. R. D. & Anderson, J. C. 1998 The metabolic cost of neural information. *Nature Neurosci.* **1**, 36–41.
- Lee, P. L. M., Richardson, L. J. & Bradbury, R. B. 2001 The phylogenetic status of the corn bunting *Miliaria calandra* based on mitochondrial control-region DNA sequences. *Ibis* **143**, 299–303.
- Leopold, A. & Eynon, A. E. 1961 Avian daybreak and evening song in relation to time and light intensity. *Condor* **63**, 269–293.
- Lindfors, P. & Tullberg, B. S. 1998 Phylogenetic analyses of primate size evolution: the consequences of sexual selection. *Biol. J. Linn. Soc.* **64**, 413–447.
- Lo Valvo, M., Rizzo, M. C., Scarabello, M. P. & Parrinello, N. 1997 Genetic variability and taxonomical considerations about six species of European Cardueline finches (Aves, Passeriformes). *Comp. Biochem. Physiol. B* **118**, 771–775.
- Mace, R. H. 1987 Why do birds sing at dawn? *Ardea* **75**, 123–132.
- McNamara, J. M., Houston, A. I. & Lima, S. L. 1994 Foraging routines of small birds in winter: a theoretical investigation. *J. Avian Biol.* **25**, 287–302.
- Marchetti, K. 1993 Dark habitats and bright birds illustrate the role of the environment in species divergence. *Nature* **362**, 149–152.
- Martin, G. R. 1990 *Birds by night*. London: Poyser.
- Martin, G. R. 1993 Producing the image. In *Vision, brain and behaviour in birds* (ed. H. P. Zeigler & H.-J. Bischoff), pp. 5–24. Cambridge, MA: MIT Press.
- Martins, E. P. 1996 *Phylogenies and the comparative method*. Oxford University Press.
- Martins, E. P. 2000 Adaptation and the comparative method. *Trends Ecol. Evol.* **15**, 296–299.
- Miller, W. H. 1979 Ocular optical filtering. In *Handbook of sensory physiology*, vol. VII/6A, ch. 3 (ed. H. Autrum), pp. 69–143. Berlin: Springer.
- Monroe, B. L. & Sibley, C. G. 1993 *A world checklist of birds*. New Haven, CT: Yale University Press.
- Motani, R., Rothschild, B. M. & Wahl, W. 1999 Large eyeballs in diving ichthyosaurs. *Nature* **402**, 747.
- Pagel, M. 1997 Inferring evolutionary processes from phylogenies. *Zoologica Scripta* **26**, 331–348.
- Price, T. 1997 Correlated evolution and independent contrasts. *Phil. Trans. R. Soc. Lond. B* **352**, 519–529.
- Purvis, A. & Rambaut, A. 1995 *Comparative analysis by independent contrasts (CAIC)*, v. 2. Oxford University Press.
- Rojas, L. M., McNeil, R., Cabana, T. & Lachapelle, P. 1999 Diurnal and nocturnal visual capabilities in shorebirds as a function of their feeding strategies. *Brain Behav. Evol.* **53**, 29–43.
- Shirihai, H., Gargallo, G. & Helbig, A. J. 2001 *Sylvia warblers*. London: Christopher Helm.
- Sibley, C. G. & Ahlquist, J. E. 1990 *Phylogeny and classification of birds*. New Haven, CT: Yale University Press.
- Slikas, B., Sheldon, F. H. & Gill, F. B. 1996 Phylogeny of titmice (Paridae): I. Estimate of relationships among subgenera based on DNA–DNA hybridization. *J. Avian Biol.* **27**, 70–82.
- Snyder, A. W., Laughlin, S. B. & Stavenga, D. G. 1977 Information capacity of eyes. *Vision Res.* **17**, 1163–1175.
- Staicer, C. A., Spector, D. A. & Horn, A. G. 1996 The dawn chorus and other diel patterns in acoustic signaling. In *Ecology and evolution of acoustic communication in birds* (ed. D. E. Kroodsma & E. H. Miller), pp. 426–453. Ithaca, NY: Cornell University Press.
- Thomas, R. J. 2000 Strategic diel regulation of body mass in European robins. *Anim. Behav.* **59**, 787–791.
- Thomas, R. J. & Cuthill, I. C. 2002 Body mass regulation and the daily singing routines of robins. *Anim. Behav.* (In the press.)

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.

Visit <http://www.pubs.royalsoc.ac.uk> to see electronic appendices to this paper.